Research Article Journal of Orthoptera Research 2026, 35(1): 23–32

Malagasy *Pseudosystolederus sikorai* Günther is *Paratettix voeltzkowiana* Saussure (Orthoptera, Tetrigidae)

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Academic editor: Maria-Marta Cigliano | Received 25 October 2024 | Accepted 6 March 2025 | Published 22 January 2026

https://zoobank.org/2E6D8F97-A8B2-44F1-95D4-81373264B235

Citation: Skejo J, Vincek N, Černila M, Ramarolahy F, Kasalo N (2026) Malagasy *Pseudosystolederus sikorai* Günther is *Paratettix voeltzkowiana* Saussure (Orthoptera, Tetrigidae). Journal of Orthoptera Research 35(1): 23–32. https://doi.org/10.3897/jor.35.140255

Abstract

The Madagascar boulder pygmy grasshopper, *Pseudosystolederus sikorai* Günther, 1939, **syn. nov.** (Tetrigidae: narrow-vertex taxa related to *Xistrella*), which is the type species of *Pseudosystolederus* Günther, 1939, is found to be conspecific with *Paratettix voeltzkowiana* Saussure, 1899. Thus, *Pseudosystolederus voeltzkowianus* (Saussure, 1899), **comb. nov.** becomes a new combination and has priority. The Madagascar boulder pygmy grasshopper is unique in its large tooth on the ventral margin of the mid femur and is relatively common on and around large boulders surrounding rivers throughout Madagascar. Photographs and measurements of the syntypes of *P. sikorai* **syn. nov.** and *P. voeltzkowianus* **comb. nov.** are presented together with new records, photographs of the species in its natural habitat, photographs of the habitat itself, and a brief discussion on the position of the genus *Pseudosystolederus* within Tetrigidae. *Morphopoides lesnei* Günther, 1979, **comb. rev.** is moved from *Pseudosystolederus* to the original combination.

Keywords

Isalo NP, Madagascar, *Morphopoides*, Nosy Be, pygmy grasshoppers, river, Tetriginae, Xerophyllini

Introduction

The diversity of pygmy grasshoppers in Madagascar is enormous, with 76 described species and many undescribed ones (Hugel 2023, Cigliano et al. 2024). In addition to taxonomic diversity, Malagasy Tetrigidae have vast functional diversity—many species are corticolous, phytophylous, ground-dwelling or leaf-litter dwelling (Krištín et al. 2019, Hugel 2023, iNaturalist 2024), but only a few are river-dependent.

The only three river-dependent Malagasy species are *Pseudosystolederus sikorai* Günther, 1939, *Morphopoides madagascariense* Günther, 1939, and *Paratettix voeltzkowiana* Saussure, 1899, with the latter, until now, being somewhat obscure. Described in 1899 by Saussure and never reported again, Günther (1939, 1974) suspected that *P. voeltzkowiana* was a senior synonym of *P. sikorai* or *M. madagascariense*. Devriese revised *Pseudosystolederus* (Devriese 1995, Devriese and Husemann 2023) and *Morphopoides* (Devriese 1999), and it became evident that *P. sikorai* and *M. madagascariense* represent two different species. However, the identity of *P. voeltzkowiana* has remained a mystery until now.

It is now time for the next step in the revision of the genus *Pseudosystolederus* Günther, 1939 and of Malagasy Tetrigidae. The aims of this paper are 1) to provide evidence that *P. voeltzkowianus* and *P. sikorai* represent a single species, 2) to provide an annotated distribution map of this species, and 3) to discuss the position of the genus *Pseudosystolederus* in light of modern Tetrigidae classification.

Materials and methods

Type specimen examination.—Syntypes of *Pseudosystolederus sikorai* **syn. nov.** are deposited in six different museums (MHNG, MNHN, MTKD, NHMUK, NHRS, and NMW; see full names below) in six different countries. The known syntypes of *Pseudosystolederus voeltzkowianus* **comb. nov.** are currently scattered across three museums (MHNG, MNCN, and SMFD) and three countries. Syntypes from all the museums were examined for this revision, and many of these are digitalized in OSF and available here: https://orthoptera.speciesfile.org/otus/808965/overview.

Morphology and measurements (Tables 1, 2) of the syntypes of both mentioned species were also compared to the holotype and paratypes of *Morphopoides madagascariense* Günther, 1939, with which *Paratettix voeltzkowiana* was also suspected to be synonymous (Günther 1939, 1974). Syntypes were also compared to the second known species of *Pseudosystolederus*, the *P. follvikae* holotype, and three new records from MNCN (Table 3).

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Abbreviations used for museums and depositories.—

ISNB	Institut Royal des Sciences Naturelles de Belgique, Brussels, Belgium
MHNG	Muséum d'histoire naturelle de Genève, Geneva, Switzerland
MNCN	Museo Nacional de Ciencias Naturales, Madrid, Spain
MNHN	Muséum national d'Histoire naturelle, Paris, France
MTKD	Museum für Tierkunde Dresden, Dresden, Germany
NHMUK	Natural History Museum, London, the United Kingdom
NHRS	Naturhistoriska riksmuseet, Stockholm, Sweden
NMW	Naturhistorisches Museum, Wien, Austria
OSF	Orthoptera Species File
SMFD	Forschungsinstitut und Naturmuseum Senckenberg, Frankfurt am Main, Germany

Terminology.—Morphological terminology follows Devriese (1991) and Tumbrinck (2014). Important diagnostic traits for the comparison were eye shape and coloration; position of the frontal costa bifurcation, antennal groove, and lateral ocelli; scutellum shape; vertex shape in dorsal view; prozona shape in lateral and dorsal view; mid femora shape; and hind tarsi characteristics.

Measurements.—Measurements were taken according to Tumbrinck (2014). The following 11 measurements were taken: **BL**, body length from the tip of vertex to the tip of pronotum; **PL**, pronotum length in dorsal view; **PLW**, width between the pronotal lobes in dorsal view; **PH**, pronotum height in lateral view; **TL**, length of tegmenula; **TW**, width of tegmenula; **AL**, length of alae (hind wings); **VW**, vertex width in frontal view; **EW**, compound eye width in frontal view; **HFL**, hind femora length; **HFW**, hind femora width.

Principal components analysis (PCA).—PCA analysis was done using ClustVis (Metsalu and Vilo 2015) to test whether *P. sikorai* **syn. nov.** and *P. voeltzkowianus* **comb. nov.** will group together or stay separate. It was also tested whether *M. madagascariense* and *P. follvikae* fall into the same group.

Taxonomy and nomenclature.—Taxonomy follows OSF (Cigliano et al. 2024). Nomenclature is in accordance with the rules of the ICZN (1999).

Literature records, new records, and georeferencing.—In addition to examination of the type series of *Pseudosystolederus sikorai* **syn. nov.**, *P. voeltzkowianus* **comb. nov.**, *P. follvikae*, and *Morphopoides madagascariense*, the literature records are compiled, new data from iNaturalist are added, and fieldwork was conducted by author JS in Ranomafana NP in January 2019 and by authors JS and FR in February 2024 in Isalo NP. All the localities were georeferenced, and the coordinates are presented next to each mentioned locality in the material examined section.

Results

Taxonomic part

Family Tetrigidae Rambur, 1838
Xistrella lineage (tribe under description)

Genus *Pseudosystolederus* Günther, 1939

Pseudosystolederus Günther 1939: 174 (description, type species: *P. sikorai* Günther 1939); Günther 1974: 982 (discussion); Devriese 1995: 102 (new combination, description of a new species); Yin et al. 1996: 904 (listed in catalog); Otte 1997: 140 (listed in catalog); Skejo 2017: 19 (mentioned); Devriese and Husemann 2023: 337 (compared to *Afrosystolederus* Devriese & Husemann, 2023); Devriese et al. 2023: 516 (included in the key to African Tetrigini); Skejo et al. 2025 (assigned to a new tribe).

Type species.—*Pseudosystolederus sikorai* Günther, 1939, **syn. nov.** of *P. voeltzkowianus* (Saussure, 1899), **comb. nov.**

Differential diagnosis.—The Malagasy genus *Pseudosystolederus* is most similar to African *Afrosystolederus* Devriese & Husemann, 2023, American *Teredorus* Hancock, 1907, Asian *Systolederus* Bolívar, 1887, and New Caledonian *Kanakacris* Kasalo & Skejo, 2025. Currently, these genera are defined geographically, and their diagnostic traits are a known problem (Devriese and Husemann 2023). Malagasy *Pseudosystolederus* members may be mistaken for *Morphopoides madagascariense* but can easily be separated by the smooth shoulders (angular in *M. madagascariense*), the presence of a single or no projections on the mid femur (two teeth present in *M. madagascariense*), the smooth external surface of the hind femora (with small projections in *M. madagascariense*), and the lack of apical teeth on the hind pulvilli (present in *M. madagascariense*). *Pseudosystolederus* can be differentiated from other Malagasy Tetrigidae by the following set of traits: very narrow vertex, narrow scutellum, short prozona, smooth shoulders, mid femora without projections or with a ventral tooth, hind tarsi with obliquely angular pulvilli without apical teeth, and brachypronotal or pauropronotal type.

Composition and distribution.—Two species endemic to Madagascar, *P. voeltzkowianus* **comb. nov.** and *P. follvikae* Devriese, 1995.

Pseudosystolederus lesnei (Günther, 1979) is moved back to *Morphopoides* because of the angled shoulders, the distal two pulvilli of the hind tarsus being equal in length and the mid femora bearing two teeth, of which one is highly reduced (see Discussion). Thus, *M. lesnei* Günther, 1979, **comb. rev.** becomes the resurrected combination.

Pseudosystolederus voeltzkowianus (Saussure, 1899), comb. nov.

Paratettix Voeltzkowiana Saussure 1899: 656 (original description, type locality: Nosy Be); Kirby 1910: 33 (listed in catalog).

Paratettix voeltzkowiana, Hancock 1907: 56 (listed in catalog); Günther 1939: 175 (mentioned as a likely senior synonym of *Morphopoides madagascariense* or *Pseudosystolederus sikorai*); Günther 1974: 982 (mentioned as a likely senior synonym of *Morphopoides madagascariense* or *Pseudosystolederus sikorai*); Skejo 2016 in OSF (Cigliano et al. 2024, mentioned as a likely member of *Pseudosystolederus*) Skejo 2017: 19 (mentioned as similar to *Pseudosystolederus*); Otte 1997: 122 (listed in catalog).

Morphopoides voeltzkowiana, Hollier 2013: 217 (syntypes from MHNG listed, mentioned combination *Morphopoides voeltzkowiana* in old OSF as nomen dubium).

Pseudosystolederus sikorai **syn. nov.** Günther 1939: 175 (original description, type locality: Madagascar, mentioned that *Paratettix voeltzkowiana* might be its senior synonym); Günther 1959: 17 (suspected as synonym of *Morphopoides madagascariense*); Günther 1974: 982 (suggested that *Paratettix voeltzkowiana* might be its senior synonym); Devriese 1995: (compared to *Pseudosystolederus follvikae*); Krištín et al. 2019: 166 (new localities); Hugel

2023: 158 (new localities); Devriese and Husemann 2023: 338 (mentioned as the type species of the genus).

Common name.—Madagascar Boulder Pygmy Grasshopper

Type locality.—MADAGASCAR: NW: Nosy Be Island (13.37°S, 48.22°E).

Original etymology.—The famous Swiss entomologists Henri Louis Frédéric de Saussure (1899) named the species after Alfred Voeltzkow (1860–1947), a German zoologist who collected the syntypes of *P. voeltzkowianus* **comb. nov.** in NW Madagascar on the island of Nosy Be.

Syntypes of Paratettix voeltzkowiana.—(Fig. 1) MADAGASCAR • 2♀, 1♂; Nosy Be ["Nossi bé" on label]; 13.37°S, 48.22°E; leg. A. Voeltzkow; MHNG • 1♀, 2♂, 1?; Nosy Be ["Nossi Bé" on label]; leg. A. Voeltzkow; SMFD • 1♂; Nosy Be ["Nossi bé" on label]; leg. A. Voeltzkow; MNCN.

Syntypes of Pseudosystolederus sikorai *syn. nov.*—(Fig. 1) MADAGASCAR • 3♀, 3♂; leg. Sikora; MHNG • 1♂;1893; leg. Sikora; MNHN • 1♂; 1894; leg. P. Camboue; MNHN •; 1♀; SE; 1926; leg. R. Decary; MNHN • 1♂; leg. Sikora; NHRS • 1♂; leg. Sikora; NHMUK • 4♀, 3♂; leg. Sikora; MTKD • 8♀, 12♂; leg. Sikora; NMW • 1♀, 7♂; Antananarivo surroundings ["Tananarive Mad" on label]; leg. Sikora; NMW.

Specific diagnosis and justification of the synonymy.—Pseudosystolederus sikorai **syn. nov.** and *Paratettix voeltzkowiana* should be regarded as conspecific because all the diagnostic characters are the same. Namely, both have mid femora with a strong ventral tooth, striped prominent eyes, black filiform antennae with pale joints between the antennomeres, a narrow vertex, a very narrow scutellum, short and depressed prozona with short prozonal carinae, relatively large tegmenula, a small depression in the metazona in the level of the tip of tegmenula, a long pronotum, and long black hindwings that usually surpass the pronotal apex (pauropronotal form) (Figs 1, 2). As both names represent the same widely distributed Malagasy species, the Madagascar boulder pygmy grasshopper, the new combination emerges: *Pseudosystolederus voeltzkowianus* **comb. nov.**

Measurements of the syntypes.—Measurements of 6 syntypes of *P. voeltzkowianus* **comb. nov.** and 7 syntypes of *P. sikorai* **syn. nov.** are shown in Tables 1, 2, respectively. PCA did not determine any morphometric difference between *P. sikorai* **syn. nov.** and *P. voeltzkowianus* syntypes (Fig. 3). Both species formed a single cluster (Fig. 3). Within the species, two clusters represent two sexes, as females (BL 13.80–16.27 mm, PL 12.28–15.44 mm, HFL 5.40–6.85 mm) are much larger than males (BL 11.40–12.97 mm, PL 10.12–12.07 mm, HFL 5.08–5.45 mm). Syntypes of *P. voeltzkowianus* **comb. nov.** did not group with *Morphopoides* (Fig. 3).

Literature records (without the types) from the oldest to the most recent.—MADAGASCAR • 2♂♂, 3♀♀; Nosy Boraha (Ile Sainte-Marie): Ikalakao Jungle: Antanandava Waterfall; 16.918°S, 49.865°E; III.1960.; leg. Andria Robinson (Günther 1974) • 1♀; Nosy Komba (between Nosy Be and Madagascar) 900 m.a.s.l. [Note: This must be an error as Mount Antagniani Omby with 622 m.a.s.l. stands as the highest point of Nosy Komba]; 13.47°S, 48.35°E; V.1956.; leg. Andria Robinson (Günther 1974) • 1♂; Arivonimamo; 18.99°S, 47.17°E; 10.X.1948. (Günther 1974) • 2♂♂, 1♀; "T. III., 173" [No specified locality]; 1894. (Günther 1974) • 3–10 specimens observed; Andringitra Catta camp S, 950–1050 m.a.s.l., rocky alpine grasslands and pastures with endemic plants; 22.084026°S, 46.772666°E; 23.3.2015 (Krištín et al. 2019) • 3–10 specimens observed; Ranomafana NP: Vohiparara trail, 1120–1200 m.a.s.l., mountain rainforest in ridge position of the National Park with many orchids; 21.238889°S, 47.393682°E; 26.3.2015. (Krištín et al. 2019) • Unspecified number of specimens; Marojejy NP: Camp 3 (= Camp Simpona), 1325 m; 14.4367°S, 49.743°E; 13.II.2018; obs. S. Hugel (Hugel 2023).

New observations (Fig. 4).—MADAGASCAR • 1♂, 1 nymph; Tsaranoro Reserve; 22.089532°S, 46.777179°E; 31.X.2014.; obs. Lemurtaquin (iNaturalist observation 35893449) • 1♂, 1♀, 8 nymphs; Lampirano; 16.824°S, 49.183°E; 8.XI.2015. obs. Nicolas Cliquennois • 9♀♀, 6♂♂; Ranomafana NP, on the boulders under the stairs under the Forêt Austral; 21.255666°S, 47.432569°E; I.2019. obs. J. Skejo, D. Kitonić (iNaturalist observations 39066695 and 42413863) • 1♂; Vohitra River; 18.919°S, 48.516°E; 27.II.2022. obs. Frank Deschandol (iNaturalist observation 144416789)

Table 1. *Pseudosystolederus voeltzkowianus* **comb. nov.** of *Paratettix voeltzkowiana*, syntype measurements. All measurements are in millimeters. First row shows the depository of each syntype, second shows sex, while the rest shows measurements in mm.

	MNCN ♂	SMFD ♂	MHNG ♂	MHNG ♀	MHNG ♀	SMFD ♀
BL	11.80	11.59	11.40	14.73	16.09	14.67
PL	10.74	10.75	10.12	13.31	14.32	13.66
PLW	3.17	3.05	3.07	4.28	4.43	3.97
PH	1.94	1.74	1.71	2.28	2.51	2.74
TL	1.41	1.48	1.70	1.87	2.11	1.94
TW	0.67	0.61	0.51	0.71	0.93	0.81
AL	9.79	9.65	10.05	12.54	13.11	12.34
VW	0.23	0.21	0.24	0.28	0.27	0.27
EW	0.66	0.68	0.70	0.71	0.78	0.69
HFL	5.17	5.22	5.19	6.73	6.18	6.44
HFW	1.78	1.72	1.65	2.13	1.92	2.14

Table 2. *Pseudosystolederus sikorai* **syn. nov.** syntype measurements. All measurements are in millimeters. First row shows the depository of each syntype, second shows sex, while the rest shows measurements in millimeters.

	NHRS ♂	NHMUK ♂	MTKD ♂	NMW ♂	MHNG ♀	MNHN ♀	MTKD ♀
BL	11.76	12.97	12.82	11.41	15.95	13.80	16.27
PL	10.85	12.07	11.80	10.73	14.71	12.38	15.44
PLW	3.15	3.36	3.19	3.05	4.35	4.00	4.20
PH	1.75	2.02	2.20	2.13	2.56	2.42	2.17
TL	1.43	1.60	1.64	1.40	1.89	1.93	1.92
TW	0.64	0.68	0.75	0.65	0.90	0.74	0.72
AL	10.03	10.53	10.48	10.08	13.36	11.43	10.49
VW	0.21	0.19	0.22	0.23	0.25	0.26	0.24
EW	0.67	0.64	0.67	0.64	0.76	0.75	0.71
HFL	5.08	5.45	5.28	5.38	6.85	6.10	5.40
HFW	1.66	1.81	1.79	1.82	2.35	2.08	1.83

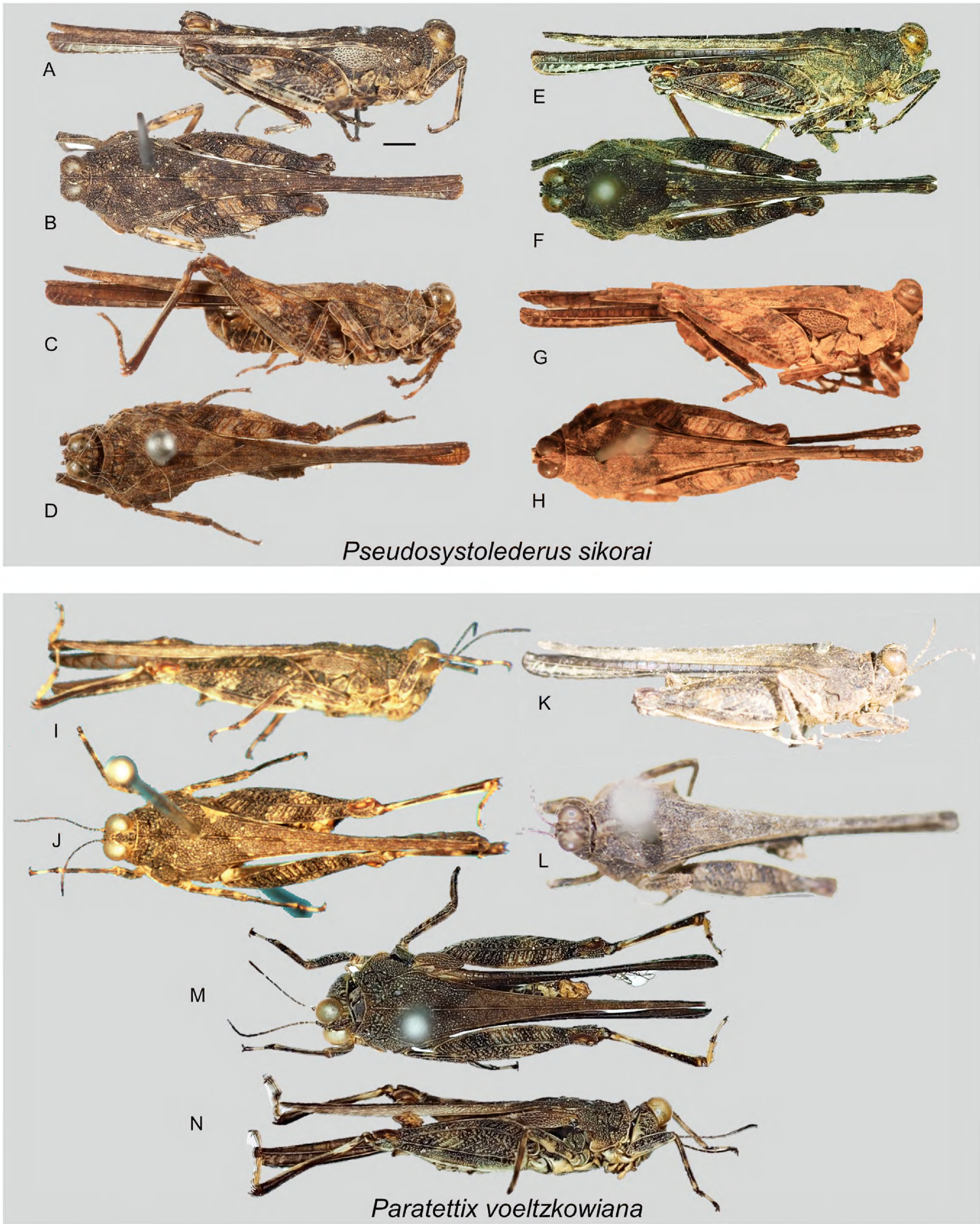

Fig. 1. Some male syntypes of *Pseudosystolederus sikorai* (**A–H**) and *Paratettix voeltzkowiana* (**I–N**). **A, B.** From NHMUK (NHMUK 010924465); **C, D.** From NHRS (NRM-ORTH 13006); **E, F.** From NMW; **G, H.** From MNHN; **I, J.** From SMFD; **K, L.** From MNCN; **M, N.** From MHNG. Photo credit **A–F, M, N**: J. Tumbrinck; **G, H, K, L**: J. Skejo; **I, J**: S. Ingrisch. Scale bar: 1 mm.

• 1♀; Anosy Region: NW from Marokibo; 24.07°S, 47.16°E; 23.XI.2020.; obs. Andrianiaina Angelo (iNaturalist observation 103386142) • 1 nymph; Menabe Region: Mahabo; 20.80222°S, 45.5495°E; 27.VIII.2022.; obs. Raphaël Grellety (iNaturalist observation 135269777) • 11♀♀, 4♂♂; Isalo NP: Namaza Canyon 780 m a.s.l.; 22.539°S, 45.382°E; II.2024.; obs. J. Skejo, Jadranka Škorput, Branko Jalžić, F. Ramarolahy (iNaturalist observations 200742554, 200742528, 200742518, and 200742515) • 1♀, 4♂♂; Isalo NP: Namaza Canyon 780 m a.s.l.; XI.2024.; 22.539°S, 45.382°E; obs. Luce Pavin, J. Skejo • 1♀; Andravelona; 18.6383°S, 47.280°E; 8.VII.2025.; obs. J. Skejo, Ivan Limić, Anton Krištin, Sitraka Tata Justin.

Distribution and habitat.—The Madagascar boulder pygmy grasshopper (*Pseudosystolederus voeltzkowianus* **comb. nov.**) is a common species in Madagascar. It is a strictly river/spring-dependent species, and it can be found on large boulders surrounding Malagasy rivers in all three main biogeographical regions (western dry, central mountainous, and eastern humid) where suitable habitats exist (Fig. 5). In the dry region, it is found syntopically with *Morphopoides madagascariense*; in the central region, it is usually found syntopically with *Paratettix scaber* and *Paratettix cinereus*, while in the rainforest region, the species can be found with *P. follvikae*, *Epitadas arius*, *P. cinereus*, and other species who live in the rainforest and who come to the proximity of water. It is worth mentioning that *P. follvikae* does not seem to be a river-dependent species, as it can also be found 40–50 m into the rainforest. The Madagascar boulder pygmy grasshopper is a good flyer and cannot be easily caught without an entomological net. The best method for recording the species is a visual search next to large water bodies surrounded by boulders and taking photographs.

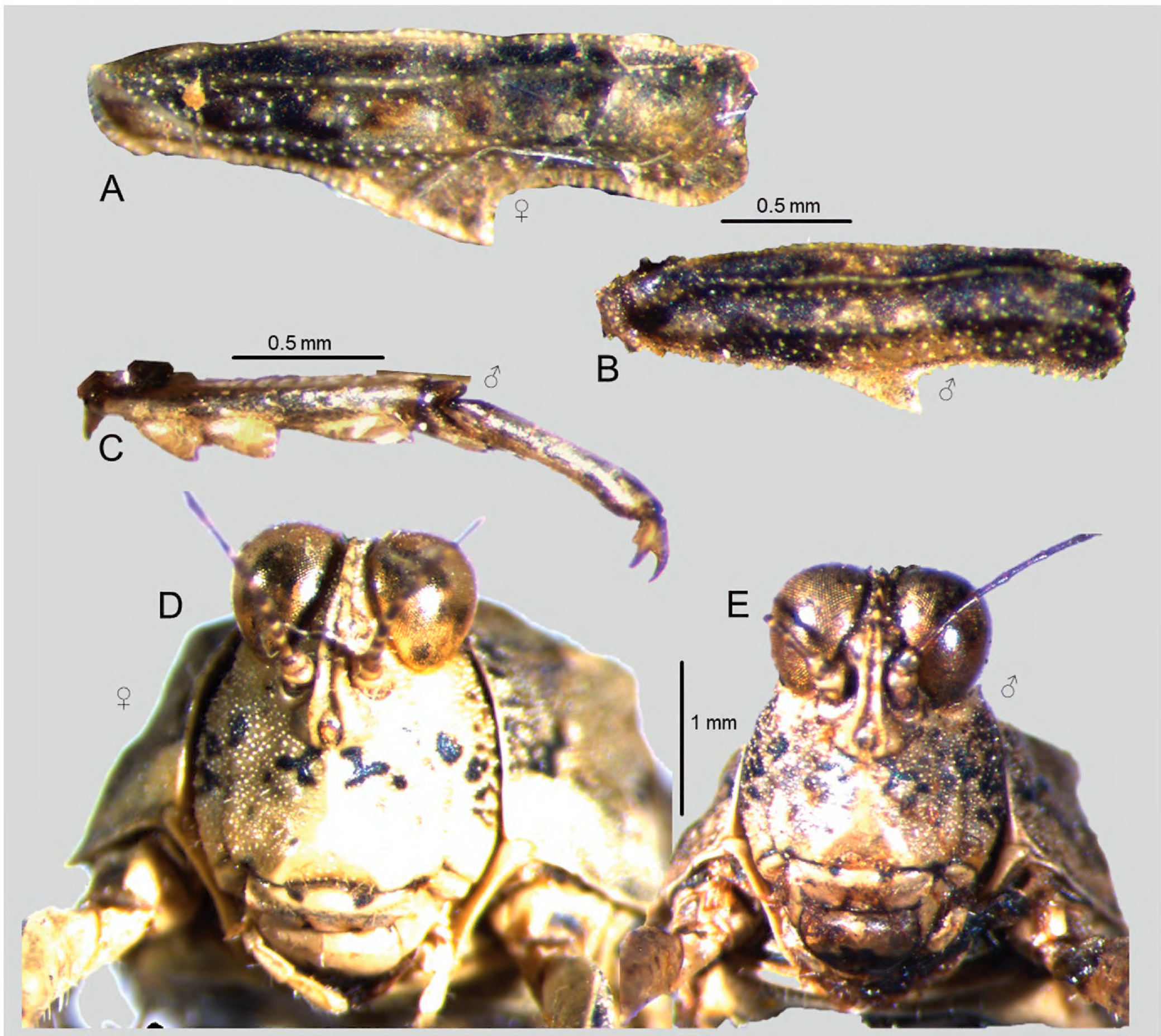

Fig. 2. The main diagnostic traits of *Pseudosystolederus voeltzkowianus* **comb. nov. A, B.** Mid femora with large ventral tooth; **C.** Hind pulvilli obliquely angular, without apical teeth, and **D, E.** Very narrow vertex and scutellum. Photo credit J. Skejo and MNCN Madrid.

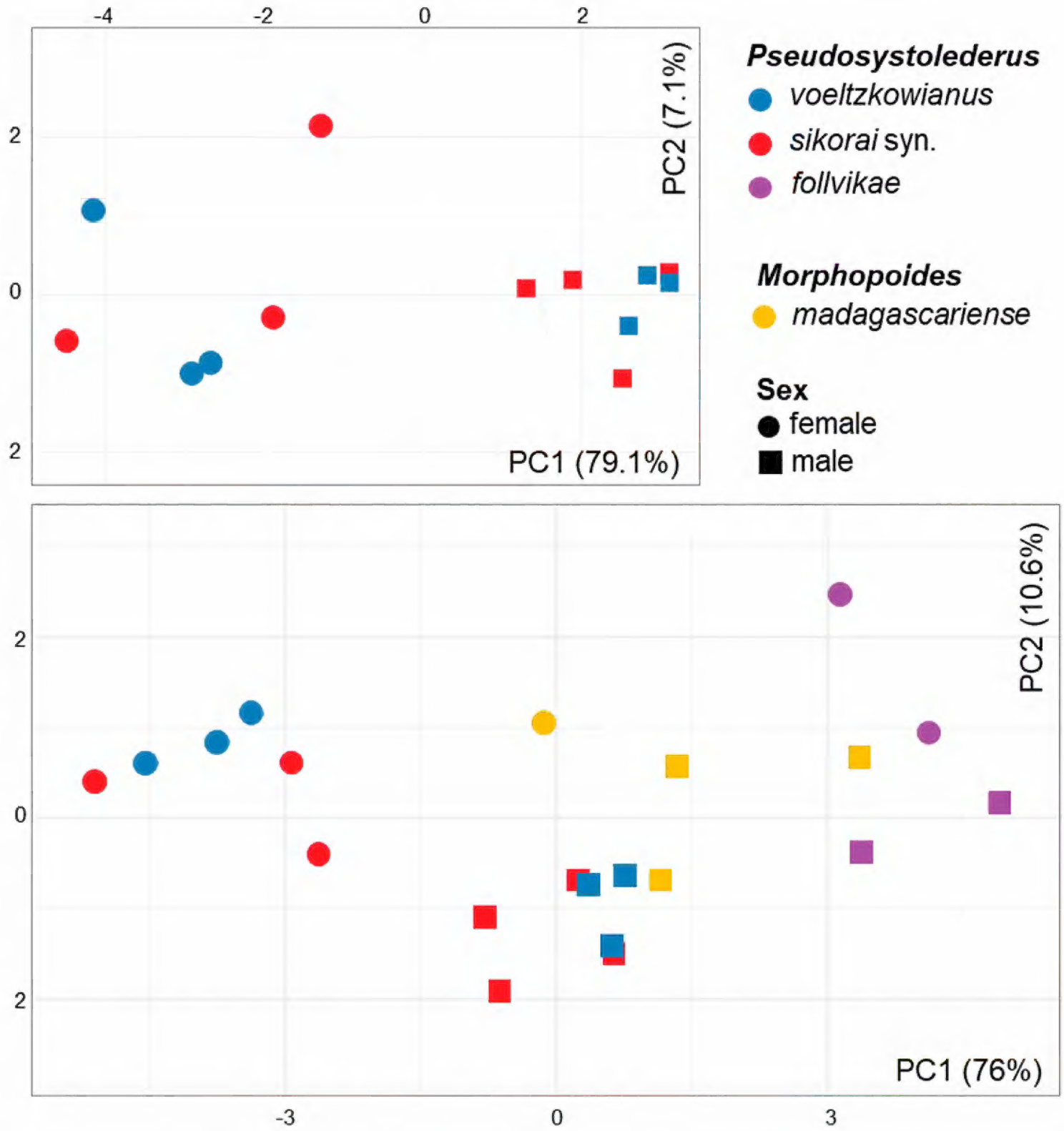

Fig. 3. Principal component analysis of the 11 measurements of *P. voeltzkowianus* (n = 6) syntypes, *P. sikorai* **syn. nov.** (n = 7) syntypes, *P. follvikae* (n = 4) holotype and three additional specimens, and *M. madagascariense* (n = 4) holotype and three paratypes. Visualized in ClustVis (Metsalu and Vilo 2015) and then uniformly recolored later.

Table 3. *Pseudosystolederus follvikae* and *Morphopoides madagascariense* measurements.

Species	*Pseudoystolederus follvikae*				*Morphopoides madagascariense*			
Type	HT	Not T	Not T	Not T	HT	PT	PT	PT
Depository	ISNB	MNCN	MNCN	MNCN	MNHN	MNHN	MNHN	MTKD
Locality	Andapa	Rogez	Fito	Fito	Nosy Be	Nosy Be	Ankazoabo	Ambovombe
Pronotum	brachy-	brachy-	macro-	pauro-	pauro-	pauro-	macro-	pauro-
Sex	♀	♀	♂	♂	♂	♀	♂	♂
BL	8.30	7.80	7.88	7.99	10.97	11.72	9.89	11.19
PL	7.20	6.79	7.11	7.23	10.28	10.98	9.25	10.54
PLW	2.80	2.84	2.41	3.37	3.13	3.46	2.83	3.06
PH	1.65	1.62	1.29	1.53	2.03	2.33	1.83	1.94
TL	1.05	1.16	1.09	1.21	1.47	1.58	1.23	1.59
TW	0.45	0.44	0.41	0.53	0.62	0.78	0.52	0.67
AL	5.55	5.21	5.91	7.94	9.31	9.87	7.84	9.22
VW	0.30	0.28	0.27	0.24	0.28	0.29	0.29	0.24
EW	0.70	0.59	0.58	0.61	0.56	0.57	0.50	0.56
HFL	4.60	4.49	4.17	4.13	4.82	5.03	4.29	4.67
HFW	1.75	1.56	1.45	1.43	1.63	1.78	1.39	1.62

Discussion

Saussure (1899) described *Paratettix voeltzkowiana* from an unspecified number of female and male individuals and without a specified type depository. During this revision, 2♀♀ and 4♂♂ syntypes were found deposited in three museums—MNCN, MHNG, and SMFD. Hollier (2013) noted that the MHNG collection Box Q5 held another 6♂♂ and 11♀♀ of Saussure's specimens with locality labels different from Nosy Be, which are thus probably not syntypes, as Saussure (1899) mentions only Nosy Be as the type locality. One syntype of unknown sex (mentioned in the OSF) from SMFD was not examined.

The syntype series of *Pseudosystolederus sikorai* originally contained 21♀♀ and 38♂♂ deposited in three museums—MHNG, MNGN, and NMW. However, during this revision, only 17♀♀ and 27♂♂ examined syntypes were found in six museums: in addition to the three mentioned, the syntypes were also found in NHRS, NHMUK, and MTD. Günther (1939) notes 8♀♀ and 16♂♂ syntypes from MHNG, of which 3♀♀ and 3♂♂ were examined for the sake of this revision. Günther (1939) also mentions 12♀♀ and 20♂♂ syntypes from NMW, while OSF (Cigliano et al. 2024) lists 9♀♀ and 19♂♂, which were examined and undoubtedly all belong to the same species. Furthermore, Günther (1939) did not mention Antananarivo as the locality, while on 8 specimens, the locality label said "Tananarive Mad."

Günther's (1939, 1974) opinion on *Paratettix voeltzkowiana* being a senior synonym of either *Pseudosystolederus sikorai* or *Morphopoides madagascariense* held only as long as the correct attribution was incomplete. As this is now done, the principle of priority applies. According to the ICZN (1999), the rules for the reversal of precedence would be met only if the senior synonym had not been used as a valid name after 1899 (Article 23.9.1.1.) and if the junior name had been used in at least 25 works published by at least 10 authors during the last 50 years without a span of more than 10 years. *Pseudosystolederus sikorai* **syn. nov.** was mentioned in the literature during the last 50 years in only 5 works by 9 authors.

Fig. 4. *Pseudosystolederus voeltzkowianus* in its natural habitat. **A.** Male from Ranomafana (photo J. Skejo); **B, C.** Females from Isalo (photo J. Skejo); **D.** Male from Tsaranoro (photo lemurtaquin, iNaturalist); **E.** Male from Alaotra-Mangoro (photo Frank Deschandol); **F.** Female from Marokibo, Ankarefo (photo Andrianiaina Angelo); **G, H.** Females from Lampirano (photo Nicolas Cliquennois); **I, J.** Nymphs from Lampirano (photo Nicolas Cliquennois).

Fig. 5. Example of *Pseudosystolederus voeltzkowianus* **comb. nov.** habitat. **A.** Large boulders in the Namaza Canyon in Isalo NP; **B.** Large boulders in the Ranomafana Canyon in Ranomafana NP. Arrows indicate places where individuals were observed standing. Photo credit J. Skejo.

Important questions that remain unanswered.—The question of whether *Systolederus*, *Teredorus*, *Pseudosystolederus*, and *Afrosystolederus* form a monophyletic group within *Xistrella* lineage or are these examples of an independent narrow vertex origin is important to answer in order to interpret the group's evolution correctly. The aforementioned genera share many similarities, but it is still not clear whether these similarities were inherited from a common ancestor. It has already been discussed (Devriese and Husemann 2023) that Tetrigidae with a very narrow vertex may be a very complex group to review taxonomically because many morphological traits related to the head have been lost or are very tricky to interpret, and the remaining ones may be superficially similar because of similar ecological niches.

This question can only be answered by a taxon-rich molecular phylogeny of Tetrigidae. The subfamily Tetriginae is currently under morphological (Subedi 2022) and molecular revisions (Kasalo et al. 2023). New genera and new species are being described (Devriese et al. 2023), while simultaneously, many synonyms are being discovered (Long et al. 2023). The issue with the position of *Systolederus* lineage within the Tetrigidae tree of life is interesting and informative, as phylogenetics sometimes reconstructs it as sister either to the tribe Tetrigini or subfamily Tetriginae (Li et al. 2020, Li et al. 2021), and sometimes as sister to the tribe Xerophyllini (Wei et al. 2023).

The last question is thus "Is *Morphopoides* a Xerophyllini member related to *Morphopus* or *Xistrella* lineage member related to *Pseudosystolederus* and *Systolederus*, or something else?" The genus *Morphopoides* is the thin border between the definitions of Tetrigini, *Xistrella-Systolederus* lineage, and Xerophyllini, so revealing its true position by molecular phylogenetics will answer many questions.

The position of *P. lesnei* has been unclear, as Günther (1979) regarded it as sister to *Morphopoides madagascariense* while Devriese (1995) moved it to *Pseudosystolederus* due to the fact that it comes in pauropronotal form, which has not been observed in Xerophyllini. We found *M. lesnei* **comb. rev.** to share an important character with some other *Morphopoides* species, namely the distal two pulvilli of the hind tarsus being equal in length and sharp, as opposed to the distal one being longer than the other two and all three blunt

in *Pseudosystolederus*. Among *Morphopoides* species, three forms of this character are observable: in some, the pulvilli are as in *M. lesnei* **comb. rev.**; in others, all three pulvilli are small, while in the type species *M. coriaceum*, the distal pulvillus is longer than the first two pulvilli, but all three are distinctly sharp. Furthermore, the mid femur of *Pseudosystolederus* species bears at most one tooth, while that of *Morphopoides* species bears at least two. In *M. madagascariense* and *M. lesnei* **comb. rev.**, the tooth at the distal part of the mid femur is reduced but still observable, unlike in *Pseudosystolederus*. Finally, *Morphopoides* species generally have their paranota pointing away from the body, while paranota point downward in *Pseudosystolederus* (and in Tetriginae in general) (Devriese 1995). In *M. lesnei* **comb. rev.**, this character most resembles the latter, while in *M. madagascariense*, it is intermediate between the two. There does not seem to be a clear line of separation between *Morphopoides* and Xerophyllini, suggesting that there may be several highly similar groups that diverged early in the evolution of the Tetriginae-Xerophyllini group. The relationships between them remain a mystery that will likely become solvable only with molecular data.

The value of the above-mentioned characters for suprageneric classification has not yet been systematically examined, but the high variability among Xerophyllini coupled with their mosaic prevalence across different taxa in different regions (pulvilli and pauropronotal forms in Tetriginae around the world, the same pattern of mid femora carination in some American Tetriginae and Metrodorinae, the same pattern of formation of pronotal humps in Tetriginae and Metrodorinae (s. l.) across the world) may suggest basal placement of Xerophyllini in the phylogeny of Tetriginae and/or Metrodorinae. If this is indeed so, finding an "unexpected" character, e.g., the pauropronotal form in *M. lesnei* **comb. rev.**, may simply reflect our lack of knowledge of the deeper branchings in the Tetriginae tree of life.

Acknowledgements

We thank all the museum curators for help during the revision of Malagasy Tetrigidae and to Hendrik Devriese for the always fruitful discussion on Tetrigidae morphology and taxonomy. Thank you also to the late Davorka Kitonić for introducing JS to Madagascar and to *Pseudosystolederus voeltzkowianus* for the first time in Ranomafana NP in January 2019. Thanks to Justin Bebert and Mladen Kučinić for organizing excursions to Isalo NP in February and November 2024 and to Jadranka Škorput, Branko Jalžić, Luce Pavin, Lazar Miletić, Jasna Hrenović, Nediljko Landeka and Domagoj Bogić for help in fieldwork and photography. Thanks to Anton Krištin, Sitraka Tata Justin, and Ivan Limić for help in the fieldwork in Andravelona in July 2025. Thanks to Tomislav Domazet-Lošo for fruitful discussions.

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